Parasitization of the Red Sunflower Seed Weevil (Coleoptera: Curculionidae) by its Larval Parasitoid *Triaspis aequoris* (Hymenoptera: Braconidae) in Cultivated Sunflower

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ABSTRACT The red sunflower seed weevil, *Smicronyx fulvus* LeConte, is a pest of sunflower in the northern and central Plains sunflower production regions. Weevil larvae feed and develop in the sunflower achene dropping to the soil to overwinter. A total of 630 parasitoids emerging from seed weevil larvae recovered from North and South Dakota and Minnesota from 1991 to 1995 was identified as *Triaspis aequoris* Martin, a solitary koinobiont endoparasitoid. The mean parasitization rate for the red sunflower seed weevil by *T. aequoris* ranged from 2.5 to 24.2% per year. There was an increase in the percentage parasitization as overall weevil populations decreased over years. In Nebraska, percent parasitization by *T. aequoris*, the only species recovered, increased with increasing densities of *S. fulvus* between 1993 and 1995. Patterns of emergence for both red sunflower seed weevil and *T. aequoris* were similar in two locations in North Dakota. Oviposition pattern in seeds in the sunflower head showed decreasing density toward the center, but *T. aequoris* parasitization was equal throughout the head. *Triaspis aequoris*, an egg-larval parasitoid, effectively searched for and attacked weevil eggs as soon as weevil oviposition had begun in the field. Date of planting studies showed that damage from weevils increased as seeding of fields was delayed, but parasitization of weevil larvae was similar among all dates. Activity by *T. aequoris* may have contributed to the decline of the red sunflower seed weevil from North and South Dakota and Minnesota. Lower densities of weevils also may account for the reduction in the diversity of parasitoid species of this weevil. The parasitoid appears to be well adapted to its host, efficiently parasitizes the red sunflower seed weevil and is amenable for use with some pest management strategies in cultivated sunflower.

KEY WORDS red sunflower seed weevil, *Smicronyx fulvus*, Curculionidae, *Triaspis aequoris*, Braconidae, biological control

THE RED SUNFLOWER SEED WEEVIL, *Smicronyx fulvus* Le-Conte, is a major economic pest of sunflower, *Helianthus annuus* L., in the northern production region of North and South Dakota, and Minnesota, (Oseto and Braness 1979, Charlet et al. 1997). The gray sunflower seed weevil, *Smicronyx sordidus* LeConte, also attacks sunflower but has been less of a problem (Charlet et al. 1997). In the central Plains the red sunflower seed weevil has been noted as a potential pest of cultivated sunflower because of increasing populations of weevils (Aslam and Wilde 1991). A native insect, the red sunflower seed weevils deposit eggs in sunflower seeds and larvae feed in the developing sunflower achenes (kernels) destroying a portion of the kernel and reducing oil content (Oseto and Braness 1980, Peng and Brewer 1995). The larvae exit the seeds in late summer and overwinter in the soil, emerging as adults the following summer. There is only one generation per year (Oseto and Braness 1979).

A number of management strategies have been investigated to prevent crop losses from this insect. These methods have included resistance in cultivated and native species (Charlet and Seiler 1994, Brewer and Charlet 1995, Gao and Brewer 1998), insecticides (Gednalske and Walgenbach 1984, Oseto and Burr 1990), trap cropping (Brewer and Schmidt 1995), tillage (Gednalske and Walgenbach 1982), and planting date (Oseto et al. 1987). There is a limited amount of information on the natural enemies of the red sunflower seed weevil. Charlet (1999) recently reviewed the known or identified parasitoids attacking the red and gray sunflower seed weevils and found reports in the literature of ≈17 species parasitizing the larvae of either one or both species. A fungus, *Metarhizum* spp., and the predators *Formica cinera montana* Emery (Hymenoptera: Formicidae), *Thereva candida* Loew, and *Fucifera rufiventris* Loew (Diptera: Therevidae) have been reported to attack weevil larvae in the soil (Pinkham and Oseto 1987).

The objectives of this study were to determine the following: (1) the species of parasitoids attacking lar-

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vae of the red sunflower seed weevil in the northern sunflower production region of North and South Dakota, and Minnesota; (2) weevil abundance and weevil parasitoids in commercial sunflower fields in Nebraska in the central Plains sunflower production area; (3) the overwintering survival and emergence pattern of the weevil and its parasitoids from the soil at two locations in North Dakota; (4) the pattern of larval parasitization and host distribution in different areas of the sunflower head (capitulum); (5) the seasonal biology of weevil parasitoids; and (6) the impact of planting date on weevil density and parasitism.

Materials and Methods

Parasitism in the Northern Plains. Physiologically mature sunflower heads were collected once between late August and early September from cultivated fields in North Dakota from 1990 to 1992, 1994, and 1995. In 1995 sunflower heads also were recovered from commercial fields in Minnesota and South Dakota. Heads were recovered early enough in the late summer to ensure that the majority of weevil larvae had not begun exiting from the seeds. Approximately 15 heads were randomly collected from each field, placed in paper bags, and returned to the laboratory. Heads were held on wire screens over large plastic pans and mature larvae were collected as they exited the seeds and dropped into the pans. Larvae were placed in covered sterilized soil-filled 1-liter plastic containers, cold-treated in the dark at 4°C for at least 16 wk to break diapause, and then held in a rearing room at 25°C, 40% RH, and a photoperiod of 15:9 (L:D) h, until the emergence of either adult weevils or parasitoids. The soil was later examined to ensure that all larvae had emerged or died. Parasitoids were collected, counted, and submitted to the USDA, ARS, Systematic Entomology Laboratory, Washington, DC, for species identification. Voucher specimens of weevils and parasitoids have been retained in the collection of the author and have been also deposited in the North Dakota State Insect Collection at North Dakota State University, Fargo, ND. Percentage parasitization was determined from the number of parasitoids recovered relative to the total number of weevil larvae reared, excluding those that died.

Weevil Abundance and Parasitism in Nebraska. A total of 15–20 sunflower heads per field was randomly collected in September in western Nebraska from 19, 18, and 10 commercial sunflower fields in 1993, 1994, and 1995, respectively. The heads were boxed and shipped to the Northern Crop Science Laboratory, in Fargo, ND, to recover weevil larvae and parasitoids. The same procedure as described earlier was used to collect and rear the exiting larvae except the sunflower heads were held separately to determine the number of seed weevil larvae per head.

Emergence Pattern of Weevils and Parasitoids. Mature red sunflower seed weevil larvae were collected from sunflower heads in research plots at Prosper, ND, and on 5–6 September 1991, were placed in 19-liter soil-filled buckets buried in the ground at Fargo and Carrington, ND. A total of 50 larvae was retained and dissected to determine the preoverwintering percentage parasitization. The buckets had the bottoms removed and replaced with wire mesh to retain the larvae but allow water to drain. Four wire-mesh covered holes were located on the sides of the buckets. The tops of the buckets were buried even with the soil surface. A total of nine buckets was buried in rows of three at each location and 1,000 newly emerged larvae were placed on the soil surface of each bucket. Although most larvae soon moved down into the soil, a thin layer of additional soil was added to the surface of each bucket to cover any remaining larvae. The following year in early June, conical wire screen cages (81 cm high by 84-cm-diameter base) were placed over each bucket. Funnels were glued to the apex of each cage and small plastic snap cap vials were inserted in the funnels to recover emerging adult weevils or parasitoids. Emergence cages were secured to the soil with metal stakes and their bases were covered with soil to prevent escape of the insects. Beginning in mid-June the cages were monitored at 5- to 7-d intervals until the end of September when emergence had ceased. Adult weevils and parasitoids were collected from each trap and the number of each recorded. Data were totaled from all nine traps. The traps were monitored again beginning in late June 1993, to determine if weevils overwintered over a period of 2 yr.

Host and Parasitoid Distribution on Plant. On 11 September 1992, five sunflower heads were randomly collected from each of the four sides and the center of a 0.5 ha research field. Each of the 25 heads was quartered and subdivided again into three cross-sections of 7–9 rows of seeds (≈2.5–3.5 cm in width). The sunflower head pollinates and the seeds fill and develop from the outside to the inside in a spiral pattern (Seiler 1997). Thus, the outermost section contains the earliest maturing seeds. Each section (five heads combined) was held separately in a plastic container until weevils had exited the seeds. The mature larvae were placed in soil and reared to the adult stage as previously described.

Seasonal Biology of Parasitoids. In 1992, a sunflower plot of ≈0.5 ha was seeded with sunflower hybrid '894' in rows 76 cm apart with plants spaced 30.5 cm within the row near Prosper, ND. Sampling began in mid-August when red sunflower seed weevil oviposition had begun. Eight to ten sunflower heads were randomly selected at 3- to 5-d intervals from the field and returned to the laboratory for examination. Subsamples of seeds were removed from the heads and those with oviposition scars (Brewer 1991) were split and examined for *S. fulvus* eggs and larvae. Because of the difficulty of locating parasitoid eggs within host eggs, weevil eggs were held on wet filter paper in sealed petri dishes until eggs hatched. First instars were then dissected and examined under a microscope for internal parasitoids. Weevil larvae dissected from seeds were grouped by head capsule width into either early (instars 1–3) or late (instars 4–5) instars and all larvae were dissected to calculate the rate of parasitism. Sampling ceased in early September when

Table 1. Parasitism of red sunflower seed weevil, *Smicronyx fulvus*, larvae by *Triaspis aequoris* collected on cultivated sunflower (*H. annuus*) in North Dakota (ND), Minnesota(MN), and South Dakota (SD), 1990 to 1995

Year	State	No. fields sampled	No. weevil larvae/head		% sites with parasitized larvae	No. weevil larvae reared	% parasitization	
			Range	Mean ± SE			Range	Mean ± SE
1990	ND	2	—	—	100	8560	11.8–17.7	14.8 ± 2.9
1991	ND	10	1.2–270.8	47.7 ± 25.6	40.0	5260	0–21.4	5.5 ± 2.7
1992	ND	3	37.4–94.0	73.0 ± 17.9	67.7	2190	0–66.7	24.2 ± 21.3
1994	ND	6	0.7–20	6.9 ± 3.2	50.0	490	0–33.3	13.9 ± 6.3
1995	ND	8	0.5–15.9	6.2 ± 2.0	62.5	745	0–40.0	13.5 ± 5.5
	MN	2	1.1–9.3	5.2 ± 4.1	50.0	156	0–25.0	12.5 ± 12.5
	SD	4	1.9–23.4	8.8 ± 5.0	25.0	526	0–10.0	2.5 ± 2.5
	Mean[a]			6.8 ± 1.8	45.8			10.2 ± 3.6

[a] ND, SD, MN for 1995.

larvae were mature and began to exit the seeds to overwinter in the soil.

Impact of Planting Date. Sunflower plots of ≈0.5 ha each were planted near Prosper, ND, 12 and 21 May and 2 June in 1992, 11 and 23 May and 3 June in 1994, and 23 May, 2 and 12 June in 1995. Seeding dates were planned to correspond to an early, mid-, and late schedule used by producers. The planting dates in 1995 were delayed because of wet soil conditions. All trials were seeded with sunflower hybrid '894' in rows 76 cm apart with plants spaced 30.5 cm within rows. Except for a fall application of herbicide, no chemical treatments were used during the growing season either year. Sunflower heads (17–29 per plot) were harvested in September as they reached physiological maturity, but before the exodus of mature larvae into the soil. Heads were returned to the laboratory and larvae were recovered and reared as previously described to determine the mean number of larvae per head and percentage parasitized. Subsamples of larvae also were collected and dissected to estimate parasitization rates for comparison with results from larval rearings.

The analysis of variance (ANOVA) option of the GLM procedure was used to compare larval numbers and rates of parasitization among the 3 yr of sampling in Nebraska, larval numbers and parasitism within three sections of the sunflower head, and among three planting dates; significantly different means were separated using least significant difference (LSD). Percentages were transformed using arc sine before analysis (SAS Institute 1990). Parasitoid species for all studies were determined by comparison with specimens identified by the Systematic Entomology Laboratory (USDA, ARS, Beltsville, MD).

Results

Parasitism in the Northern Plains. More than 20,000 red sunflower seed weevil larvae were collected from sunflower heads and reared between 1990 and 1994 from North Dakota and from North Dakota, Minnesota, and South Dakota in 1995. All of the 630 parasitoids emerging from the weevil larvae in the samples were identified as *Triaspis aequoris* Martin, a solitary endoparasitoid and only females were recovered (Table 1). This species of parasitoid was originally de-

scribed from a female collected in Kansas and no host was given (Martin 1956). Populations of *S. fulvus* in the samples taken from North Dakota were highest in 1991 and 1992, with mean densities of 48 and 73 larvae per head, respectively. Numbers declined in 1994, with an average of only seven larvae per head. The following year densities were again low with a mean of only five to nine larvae per head in the three states sampled. With the exception of South Dakota, 40% or more of the fields sampled had parasitized larvae. The mean parasitization rate for the red sunflower seed weevil ranged from 2.5 to 24.2% per year for the 5 yr of the study (Table 1). In North Dakota, populations of *T. aequoris* increased in the study sites from 1991 to 1995. The percentage of sites with parasitized larvae rose from 40% in 1991 to >60% in 1995. Parasitization of larvae in North Dakota did not diminish over time even though weevil densities were decreasing.

Weevil Abundance and Parasitism in Nebraska. Red sunflower seed weevils were recovered from the majority of the fields sampled during each of the 3 yr of the study (Table 2). The rate of infestation of sunflower heads increased each year with weevil densities of 36 larvae per head in 1995 almost three times higher than were present in 1993. The increase in weevil populations in Nebraska was in contrast to North Dakota where weevil density declined in fields sampled from 1991 to 1995 (Table 1). Over 16,000 weevil larvae were reared from 1993 to 1995. Only one species of parasitoid was recovered, *T. aequoris*, and rates of parasitization averaged from 1.6% in 1994 to >16% in 1995. Parasitization rates in 1994 were much lower than those in North Dakota, but in 1995 they had increased significantly and were similar to parasitization rates recorded in North Dakota (Table 1).

Emergence Pattern of Weevils and Parasitoids. A total of 223 and 233 weevil adults and parasitoids emerged from the 9,000 larvae placed in soil-filled buckets at Fargo and Carrington, ND, in 1992, respectively. The sex ratio of red sunflower seed weevils was 2.3:1 females to males. *Triaspis aequoris* was the only species of parasitoid recovered at either study site and no males emerged. Based on the number of parasitoids emerging, the parasitization rate (calculated from all weevil larvae placed in buckets) was 2.2% for Fargo and 1.0% for Carrington, even though the weevils used in the study were collected from the same location. It

Table 2.   Number of red sunflower seed weevil larvae per head and larval parasitization rate by *Triaspis aequoris* collected on cultivated sunflower (*H. annuus*) in western Nebraska, 1993 to 1995

Year	No. fields sampled	No. weevil larvae/head		No. weevil larvae reared	% parasitization	
		Mean ± SE	Range		Mean ± SE	Range
1993	19[a]	14.1 ± 3.4a	1.5–55.7	3,348	3.9 ± 2.4a	0–33.3
1994	19	26.1 ± 5.1b	0.7–83.4	7,508	1.6 ± 0.8a	0–12.5
1995	13[b]	36.5 ± 13.3b	0.6–130.3	5,472	16.6 ± 12.1b	0–100

Means followed by the same letter within the same column are not significantly different ($P < 0.05$) using LSD. Percentages transformed using arcsine.
[a] Three fields had no larvae detected.
[b] Two fields had no larvae detected.

is possible that differences in soil types might have influenced the emergence. Preemergence dissection of larvae used in the study showed that 6.0% of red sunflower seed weevil larvae actually were parasitized.

At Fargo, weevil adults emerged over a 1-mo period, from 6 August through 4 September, with most emerging in late August (Fig. 1). Parasitoid emergence at Fargo closely followed the weevil emergence pattern although some were still emerging from the soil until later September. Weevil emergence was more protracted at the Carrington location, beginning a few days earlier and extending almost until the end of September (Fig. 1). But, ≈80% had emerged by the

end of August at both locations. Parasitoid emergence at Carrington was more rapid than at Fargo, occurring over a 3-wk period with 100% emerged by the end of August.

Host and Parasitoid distribution on Plant. Oviposition by female red sunflower seed weevils, as revealed by the number of mature larvae recovered from the seeds, showed a definite pattern of decreasing density progressing from the outer portion of the head toward the center (Table 3). The progression of flowering, seed filling, and development by the sunflower head also proceeds from the margin to the center of the head. However, the only significant difference was between the outer section of seeds compared with the middle and inner sections. Parasitization of the larvae did not differ among the three areas of the head studied with an average of 33% of the larvae attacked. *Triaspis aequoris* was the only parasitoid species recovered from the reared red sunflower seed weevil larvae. Results showed that *T. aequoris* was present throughout the seed weevil oviposition period and attacked larvae in all portions of the sunflower head.

Seasonal Biology of Parasitoids. In 1992, *T. aequoris* was present early in the season as shown by the 65% parasitization rate for weevil eggs collected on 14 August at Prosper, ND (Table 4). The parasitoid was observed actively ovipositing in the field during the entire time eggs were sampled from sunflower seeds. The final determination of parasitism (30%) on 4 September was made in mature weevil larvae that were dropping from sunflower heads to the soil to overwinter. *Triapis aequoris* appears to be a solitary egg-larval endoparasitoid because only one parasitoid larva was present in each weevil larva dissected. The
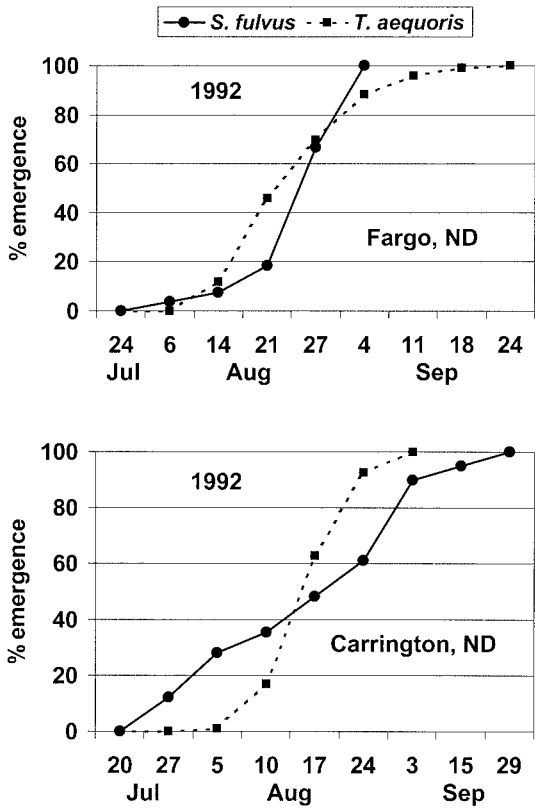

Fig. 1.   Emergence pattern of adult red sunflower seed weevil and its parasitoid, *Triaspis aequoris*, at Fargo and Carrington, ND, 1992

Table 3.   Distribution pattern of red sunflower seed weevil larvae on sunflower heads and parasitization of weevil larvae by *Triaspis aequoris*, Prosper, ND, 1992

Head section	No. heads	Weevil larvae per section of head		% parasitization	
		Mean ± SE	Range	Mean ± SE[a]	Range
Outer	25	109.8 ± 38.4a	11–205	40.7 ± 8.4a	18.2–68.6
Middle	25	29.8 ± 7.7b	5–45	25.8 ± 10.4a	0–45.0
Inner	25	3.0 ± 2.1b	0–11	28.6 ± 28.6a	0–57.1
Mean		47.5 ± 17.1		33.1 ± 6.7	

Means followed by the same letter within a column are not significantly different ($P < 0.05$) using LSD.
[a] Data analyzed using arcsine transformation.

Table 4. Number of red sunflower seed weevil eggs and larvae dissected and percentage parasitization of *S. fulvus* stages by *Triaspis aequoris*, Prosper, ND, 1992

Sampling date	*S. fulvus* stage							
	Egg		Instars 1–3		Instars 4–5		Total	
	No.	%	No.	%	No.	%	No.	%
14 Aug	40	65.0	—	—	—	—	40	65.0
19 Aug	25	36.0	11	36.4	—	—	36	44.4
21 Aug	25	68.0	32	65.6	8	50.0	65	67.7
26 Aug	—	—	15	13.3	18	61.1	33	39.4
4 Sep	—	—	—	—	50	30.0	50	30.0

only parasitoid eggs detected were in first instar weevils hatched in the laboratory from weevil eggs recovered in sunflower seeds.

Impact of Planting Date. Among the 3 yr studied, red sunflower seed weevil densities were greatest in 1992 (Table 5). The latest planted sunflowers in 1992 (2 June) had significantly higher levels of seed weevil larvae per head compared with those of the first two dates. Although populations of the weevil were greater in the latest planting date, the numbers were not sufficient to cause a significant difference in the percentage of seeds damaged. In 1994, there was no significant difference between the first and latest planting dates, but the middle date had lower weevil numbers compared with the first planting date. Damage, however, was too low to compare the dates of planting. In 1995, although weevil numbers were again low, the pattern of higher populations as planting date was delayed was evident as in 1992. The percentage of seed damaged was very low, but the latest planting date (12 June) did have significantly more damage. This was evident even though the dates of planting had been shifted even later due to wet soil conditions.

Parasitization among the different planting dates based on parasitoid emergence from collected larvae showed no significant difference in any of the 3 yr studied (Table 5). Again, *T. aequoris*, was the only parasitoid species recovered from red sunflower seed weevil larvae. Parasitization rates varied from 4 to 23%

of larvae parasitized by *T. aequoris* among planting date. Two dates had insufficient larvae for rearing to determine parasitism. However, rates of parasitization calculated from dissected larvae were much higher than those from reared larvae. This indicates that relying on data only from rearing underestimates the impact of the parasitoid. Part of the problem is the difficulty in being able to successfully break diapause and rear the host. Under laboratory conditions mortality during rearing was very high. A lower estimate of parasitism can result if parasitized individuals suffer a proportionally greater mortality during rearing. Thus, Day (1994) proposed using both methods to provide more accurate data on the activity of diseases or parasitoids.

Discussion

The diversity of parasitoids reported to attack the red sunflower seed weevil larvae (Charlet 1999) was not evident in the current study where only the braconid *T. aequoris* was reared from the thousands of larvae collected from cultivated sunflower fields in North and South Dakota, Minnesota, and Nebraska. To date, *T. aequoris* has only been reared from *S. fulvus* and possibly *S. sordidus*, weevils that attack sunflower and a few related composite weeds (Charlet and Seiler 1994). Additional species of parasitoids reared from red sunflower seed weevil infested seeds included *Eupelmus amicus* Girault (Eupelmidae), *Eurytoma* sp. (Eurytomidae), *Zatropis incertus* (Ashmead) (Pteromalidae), *Torymus capillaceus albitarsis* (Huber) (Torymidae) in Illinois (Bigger 1930, 1931, 1932, 1933). Although earlier studies from cultivated sunflower in North Dakota yielded the pteromalids *Trimeromicrus* sp. (probably *T. maculatus* Gahan) and *Pteromalus* sp., and the braconids *Bracon mellitor* Say and *Nealiolus curculionis* (Fitch) (Oseto and Braness 1979, Pinkham and Oseto 1987, Charlet 1999), none of these species were recovered in sampling from any of the locations in the study reported here. One possible reason could

Table 5. Number of red sunflower seed weevil larvae per head, percentage of seed damaged per head, number of larvae reared or dissected, and larval parasitization rate of *Triaspis aequoris* reared from *S. fulvus* for three different planting dates at Prosper, ND, in 1992, 1994, and 1995

Year	Planting date	No. heads	No. *S. fulvus* larvae collected per head (Mean ± SE)	% *S. fulvus* damaged seeds	% parasitization	
					No. larvae reared	Mean ± SE
1992	12 May	20	10.6 ± 2.7a	3.1 ± 0.7a	211 (50)	12.7 ± 8.0a (30.0)
	21 May	20	11.8 ± 3.9a	2.2 ± 0.7a	235 (50)	7.7 ± 7.1a (10.0)
	2 June	20	43.3 ± 12.5b	4.5 ± 1.6a	865 (96)	20.6 ± 7.2a (29.2)
1994	11 May	29	7.1 ± 2.7a	1.4 ± 0.2	205 (23)	4.1 ± 2.5a (43.5)
	23 May	19	0.2 ± 0.2b	0[1]	3 (7)	0a (28.6)
	3 June	17	2.2 ± 1.0ab	0[1]	30 (22)	22.7 ± 15.7a (9.1)
1995	23 May	30	0.03 ± 0.03a	0a	1	0a
	2 June	29	1.2 ± 0.5a	0.2 ± 0.2a	34	6.3 ± 6.3a
	12 June	32	8.0 ± 2.3b	1.0 ± 0.3b	256	7.0 ± 6.2a

Numbers in parentheses represent *S. fulvus* parasitization rate based on dissection of red sunflower seed weevil larvae. Means followed by the same letter within the same column and within years are not significantly different ($P < 0.05$) using LSD. Percentages transformed using arc sine. No larvae were dissected in 1995 because of limited numbers available.

[a] Less than 0.1% damage.

be the lower weevil populations encountered in the fields sampled in the current study compared with those that occurred in the 1980s and early 1990s when many fields in the northern Plains production region had economic levels of *S. fulvus* (Brewer and Glogoza 1997). The economic threshold (depending on price, plant population, and treatment costs) for oilseed sunflower may be in the range of 5–9 adults per plant or ≈122–223 larvae per head (Peng and Brewer 1995). Populations in the North Dakota fields sampled, with the exception of a few fields sampled in 1991, were all well below this level (Table 1). Hawkins (1994) suggested that abundant herbivores should accumulate more parasitoid species because they would be encountered more frequently and also that changes in abundance over short time periods can impact species richness. This was the first report for larval parasitoids of the red sunflower seed weevil from cultivated sunflower in South Dakota, Minnesota, and Nebraska, so conclusions cannot be drawn about the diversity of species recovered in these states.

Red sunflower seed weevil larvae recovered from native sunflowers in the northern and central Plains also were attacked by a greater species diversity of parasitoid species than was evident in the current study from cultivated sunflower fields (Charlet and Seiler 1994). These included the braconids *N. curculionis*, *N. rufus* (Riley) and *Urosigalphus femoratus* Crawford and the pteromalids *Mesopolobus* sp. and *T. maculatus*. The weevils *S. fulvus* and *S. sordidus* occurred together in some samples and it was speculated that the parasitoids *N. rufus* and *U. femoratus* actually could be attacking the latter species (Charlet and Seiler 1994). It is evident from this study that although there is a diversity of species reported as parasitoids of the red sunflower seed weevil, they are either now so rare they were not detected in the sampling, are not adapted to the region, or perhaps have been displaced by *T. aequoris*.

Parasitism of *S. fulvus* larvae in North Dakota sunflower fields by *T. aequoris* may have had a role in the decline of this pest. Overall populations of the weevil decreased over the years in which sampling occurred (Table 1), but parasitism was not diminished, showing the ability of the parasitoid to effectively forage for weevils even at very low population levels. The actual parasitization rates are likely underestimated based on comparisons of rearing and dissection conducted for the planting date study (Table 5). Impact by *T. aequoris* on red sunflower seed weevil populations in Nebraska increased over time as indicated by the range of infestation levels seen in the 3 yr of collections; weevil populations were almost three times higher in 1995 as were noted in 1993, and there was a significant increase in parasitization rate (Table 2).

Triaspis aequoris overwinters within the fifth instar of the weevil red sunflower seed weevil larva in the soil and both host and parasitoid emerge the following summer. Although there has been speculation that the weevil could survive over more than one season, the data from this study showed that neither adult weevils nor parasitoids emerged during the second year. Fur-

ther investigations are needed to confirm whether survival over one season is possible because the percentage recovery in my study was very low. Emergence patterns studied at two locations in North Dakota showed that the parasitoid emerged slightly later than the weevil, but the rate of emergence was then similar to *S. fulvus* (Fig. 1). This pattern of weevil emergence was somewhat different than that reported by Oseto and Korman (1986) and Pinkham and Oseto (1987) who noted that weevils began emerging in early to mid-July and by the end of July most had emerged from the soil. However, a study from South Dakota showed that the majority of weevils had not emerged from the soil until mid-August (Gednalske and Walgenbach 1982). It is likely that temperature, soil type, and moisture conditions could account for the differences.

The female weevils need to consume pollen from blooming sunflowers for egg maturation to occur before egg deposition in the sunflower seed (Korman and Oseto 1989, Rana and Charlet 1997). *Triaspis aequoris*, appears to be well adapted to the phenology of its host, because females are actively search for the host and ovipositing in eggs or early instars of *S. fulvus* when weevils are first present on sunflower heads. Host synchronization, as noted by Godfray (1994) is especially important for the success of the natural enemy when the host has one or only a few generations per year. A study of the emergence of *S. fulvus* and another parasitoid, *N. curculionis*, in North Dakota by Pinkham and Oseto (1987) noted poor synchrony of parasitoid and host with peak emergence of the parasitoid ≈30 d after that of the red sunflower seed weevil adults, and may be the reason none were collected in the current study.

The pattern of weevil oviposition which results in a decreasing number of larvae toward the center of the sunflower head exhibited by the red sunflower seed weevil revealed the preference of the female weevil for heads shedding pollen (Table 3). This pattern also was noted by Brewer (1991) who remarked that because the female deposits eggs in seeds of intermediate (achene with partially developed embryo) maturity the female leaves the head before some of the seeds in the middle rows and most of the seeds in the inner rows have reached the stage preferred for egg laying. *Triaspis aequoris* did not display a location preference and parasitized weevils in all sections of the sunflower head, demonstrating that the parasitoid was present and actively searching for its host during the entire period of weevil activity. Sampling of weevil eggs and larvae from field plots also confirmed that *T. aequoris* successfully searched for, located, and parasitized *S. fulvus* throughout the period that eggs and larvae were present in the sunflower seeds (Table 4).

Although declining red sunflower seed weevil populations over time impacted date of planting studies between 1992 and 1995, there was still evidence that damage from larval feeding was higher on later-seeded sunflower (Table 5). Oseto et al. (1987) also noted that later planting dates had higher damage due to the occurrence of sunflower heads at a susceptible stage

during the period of maximum weevil activity, evidence for the use of altered planting dates as a cultural control strategy in an integrated pest management (IPM) program for *S. fulvus.* Although larval densities were different among planting dates, the lack of the significant difference in the rates of parasitization again showed that the seed weevil parasitoid, *T. aequoris*, was able to search for its host over a wide range of population sizes and over a long period of time, because sunflowers from the three dates of planting would be blooming and setting seed for many weeks. Thus, the parasitoid could be effective in combination with planting date, a cultural control strategy of IPM, used to manage seed weevil populations.

Triaspis aequoris was the only parasitoid detected attacking the red sunflower seed weevil in cultivated sunflower in the northern Plains sunflower production region and into Nebraska, which occupies the northern portion of the central Plains production region. Activity by this parasitoid, may have contributed to the decline of the weevil and its damage from North and South Dakota and Minnesota. Lower densities of weevils may also account for the reduction in parasitoid species richness reported earlier. Studies on seasonal abundance, planting date, emergence, and distribution of parasitization on the sunflower head revealed that *T. aequoris* is well adapted to its host and is an efficient egg-larval koinobiont, endoparasitoid of the red sunflower seed weevil in cultivated sunflower.

Acknowledgments

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